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Proceedings of the Workshop on the Potential use of the Biomass-size Spectrum for Estimating Northern Cod Stocks. Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, March 25-27, 1991

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Fisheries and Aquatic Sciences 1844

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PROCEEDINGS OF THE WORKSHOP ON THE POTENTIAL USE OF THE BIOMASS-SIZE SPECTRUM FOR ESTIMATING NORTHERN COD STOCKS

Northwest Atlantic Fisheries Centre
St. John's, Newfoundland
March 25-27, 1991

Edited by

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ABSTRACT

Paranjape, M. A., and R. W. Sheldon [ed.]. 1991. Proceedings of the workshop on the potential use of the biomass-size spectrum for estimating northern cod stocks. Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, March 25-27, 1991. Can. Tech. Rep. Fish. Aquat. Sci. 1844: iv + 43 p.

An international workshop on the potential use of the biomass size spectrum concept to estimate and predict standing stock levels of northern cod was held on March 25-27, 1991, at the NAFC, St. John's, Newfoundland. This workshop was one of the several held under the auspices of Northern Cod Science Program before new research initiatives were begun. The aim of this workshop was to bring together authorities recognized in the various fields to:

1. review the present state of knowledge;

2. discuss aspects of biomass descriptions and predictions based on contemporary studies of the marine and freshwater ecosystems;

3. assess the feasibility of understanding the dynamics of fish producing ecosystems from a knowledge of food web structure at the lower trophic levels; and

4. attempt a consensus and assess the feasibility of using the biomass size spectrum approach for a study of northern cod.

Over 50 people participated in the workshop. Representatives from Scotia-Fundy, Quebec (DFO), Memorial University, Dalhousie University, University of Toronto, University of Maryland, government research laboratories from U.K., Poland, South Africa, as well as many members of DFO Newfoundland Region were present. The program consisted of a mix of formal presentations and open discussions, followed by deliberation of three panels of experts to produce recommendations for the conduct of future research. Highlights of the workshop are recorded in these proceedings.

RÉSUMÉ

Paranjape, M. A., and R. W. Sheldon [ed.]. 1991. Proceedings of the workshop on the potential use of the biomass-size spectrum for estimating northern cod stocks. Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, March 25-27, 1991. Can. Tech. Rep. Fish. Aquat. Sci. 1844: iv + 43 p.

Un atelier interational sur la possibilité d'utiliser le concept de spectre de taille de la biomasse pour évaleur et prédire les niveaux de stocks actuels de morue du Nord a eu lieu du 25 au 27 mars 1991 au CPANO de St. John's (Terre-Neuve). Cet atelier faisait partie de nombreuses activités menées sous les auspices du Programme scientifique de la morue du Nord, avant la mise en vigueur de nouvelles initiatves de recherche. Le présent atelier visait à réunir des spécialistes reconnus dans divers domaines aux fins suivantes:

1. faire le point sur les connaissances actuelles;

2. à partir de récentes recherches sur les écosystèmes marins et d'eaux douces, aborder divers aspects des descriptions et des prédictions de biomasses;

3. évaluer la possibilité de comprendre la dynamique des systèmes producteurs de poissons en étudiant la structure des réseaux alimentraires du niveau trophique inférieur; et

4. tenter d'arriver à un consensus et évaluer la possibilité d'utiliser l'approche du spectre de taille de la biomasse pour étudier la morue du nord.

Plus de cinquante personnes ont participé à l'atelier. Il s'y trouvait notamment des représentants de Scotia-Fundy, du Québec (MPO), de l'Université Memorial, de l'Université Dalhousie, de l'Université de Toronto, de l'Université du Maryland, des laboratoires gouvernementaux de G.-B., de Pologne, de d'Afrique du Sud, ainsi que des délégués du MPO de la région de Terre-Neuve. L'atelier consistait d'un mélange de conférences et de délibérations par trois groupes de spécialistes qui ont abouti à formuler des recommandations en vue de prochaines recherches. Les points saillants de l'atelier sont décrits dans le présent compte rendu.

PROGRAM SCHEDULE

MONDAY, MARCH 25

09.00-09.10	Welcome by the Regional Director, Science, DFO	L.W. Coady
09.00-09.15	Introduction	R.W. Sheldon

RECENT RESEARCH ON BIOMASS DISTRIBUTIONS
Chair - M. A. Paranjape

09.15-09.35	Towards a theory of the body-size spectrum of in aquatic systems	L. M. Dickie
09.35-09.55	Dynamic simulation modelling of biomass spectra	W. Silvert
09.55-10.15	Biomass spectra as indices of ecosystem production in relation to fisheries yield	P. Boudreau
10.15-10.35	Coffee	
10.35-10.55	Microplankton biomass distributions of three contrasting ecosystems in the southern Bengula Region	C. L. Moloney
10.55-11.15	Size structure of the southern Baltic ecosystem	Z. Witek
11.15-11.35	Particle size and fish larval distributions in the Irish Sea	K. Brander
11.35-11.55	Length abundance and distributions of demersal fishes on the Scotian Shelf	J. de Aracama
11.55-12.15	Effects of fishery exploitation on the size structures of northern cod stocks: a preliminary analysis	S. R. Kerr
12.15-12.35	Biomass size distribution and metabolism in the pelagic zone	R. Quiñones

L U N C H

APPLICATIONS
Chair - M. A. Paranjape

13.30-13.55	Biomass size spectra of the Lake Michigan pelagic food web	W. G. Sprules
13.55-14.20	Size spectra in deep demersal fishes	R. Haedrich
14.20-14.45	Biomass spectra and fish catches in the North Atlantic	R. W. Sheldon, M. A. Paranjape

14.45-15.10	The biomass spectrum in the S.E. Atlantic in relation to historic and potential pelagic fish yields	J. G. Field, C. L. Moloney
15.10-15.35	The allometric determination of pelagic production rates	I. R. Joint
15.35-16.00	Tea	
16.00-	General discussion limited to matter arising from the presentations	

TUESDAY, MARCH 26

BACKGROUND FOR UNDERSTANDING THE NORTHERN COD ECOSYSTEM
Chair - M. A. Paranjape

09.00-09.30	The physical environment of the Northern Cod ecosystem	S. Narayanan
09.30-10.00	Patterns of recruitment variation: influence of life-history and environments	R. Myers
10.00-10.30	Pelagic fish populations of the Grand Banks region	G. H. Winters
10.30-10.50	Coffee	
10.50-11.20	The production system supporting cod in Div. 2J3KL	G. R. Lilly
11.20-11.50	Investigating the effects of the Hudson Strait outflow on the Labrador Shelf using the biomass size spectrum	K. Drinkwater G. Harding L. M. Dickie R. W. Sheldon
11.50-12.20	Quantitative survey data for benthic production estimates	D. Peer, P. Schwinghamer
12.20-12.50	Size- and biomass-distribution of pelagic zooplankton on the SE Shoal of the Grand Bank	C. Taggart, K. Frank J. Carscadden, W. Leggett

LUNCH
STRUCTURED DISCUSSION

14.00- 1) How well can we extrapolate from the size distribution of small organisms to estimate fish stocks?

Discussion Panel: W. G. Sprules (Rapporteur)
S. R. Kerr
L. M. Dickie
J. G. Field

2) How well can we estimate fish stocks from fisheries data?
Discussion Panel: K. Brander (Rapporteur)
B. Atkinson
P. Shelton
J. Carscadden

3) Is either 1) or 2) relevant to fisheries prediction?

Open discussion: All participants

WEDNESDAY, MARCH 27

RECOMMENDATIONS FOR FUTURE RESEARCH

This will consist of a morning session where three committees will address the problem separately and an afteroon session where all the participants will discuss the (widely differing?) recommendations of the committees.

09.00-12.30 Meetings of the working groups.

LUNCH

14.00- Summary and general discussion of research recommendations (All Participants)

PROCEEDINGS OF THE WORKSHOP ON THE POTENTIAL USE OF THE BIOMASS-SIZE SPECTRUM FOR ESTIMATING NORTHERN COD STOCKS

NORTHWEST ATLANTIC FISHERIES CENTRE, ST. JOHN'S, NEWFOUNDLAND MARCH 25-27, 1991

Preamble

To the lover of prescribed routine methods with the certainty of 'safe' results the study of ecology is not to be recommended.

(after Tansley from Elton, 1927, p.4)

This report has been organized so that the recommendations of the ecologists who attended the workshop can be easily appraised. We start with the abstracts of each of the individual presentations. This is followed by the summaries of two "question and answer" sessions, based on the themes 1) how well can we extrapolate from the size distribution of small organisms to estimate fish stocks?, and 2) how well can we estimate fish stocks from fisheries data? We then present the details of the recommendations of each of three specialist working groups. Finally, we present our overall summary of their recommendatons.

INTRODUCTION

The organization of this workshop was a little different from the normal "run of the mill" affair. We did not get together to present the latest hot news of our research, although some of us did this; our prime purpose was to teach each other and to learn from each other. Our ultimate aim was to provide advice on whether it would be worthwhile to spend a large amount of money on biomass spectrum research in an attempt to improve our ability to estimate fish stocks.

We have come a long way since the first presentation of the biomass spectrum hypothesis twenty years ago. Those were the days when Gordon Riley was unconvinced and said that it was nothing more than an Eltonian pyramid. And he was right. The Eltonian pyramid and the biomass spectrum use the same data to describe ecosystem structure. But there are certain advantages to the biomass spectrum approach, particularly to non-mathematicians. The biomass spectrum essentially describes a linear relationship between biomass and size. And as we explain in response to the "it's only an Eltonian pyramid" criticisms, one can extrapolate straight lines fairly easily but pyramids are rather more difficult.

The biomass spectrum hypothesis is now generally accepted by ecologists as a reasonable way to describe aquatic ecosystem structure. But the concern of the workshop was not whether the hypothesis was reasonable or valid. We needed to know if it was useful.

To illustrate this we could profitably draw on a parallel example. Consider the Copernican view of the universe. Most people would agree that this is a valid way to describe the universe. But professional navigators (and members of the flat earth society) would strongly disagree. If one has to navigate a ship from St. John's to Rotterdam using a sextant and a chronometer, the Copernican description of the universe is not going to be very useful. Astronomers, on the other hand, would not doubt the validity of the Copernican system. Their science is entirely based on it. Both views are valid but astronomers and professional navigators just look at the universe from different viewpoints.

We face the same kind of problem with the biomass spectrum. There is little doubt that the hypothesis is valid, but now useful is it beyond academic ecology? This was the question we tried to answer. If it could be shown that useful estimates of fish stocks could be made from observations of the biomass spectrum, then the work of stock assessment scientists could perhaps be made a little easier. If, on the other hand, we found that the stock assessment scientist turns out to be comparable to our navigator, to whom biomass spectrum observations are interesting but not particularly useful, we could save the Canadian Government a considerable amount of research funding. This, ultimately, was the reason for the workshop.

We structured the workshop to address this problem, and we were particularly interested in the application of the biomass spectrum hypothesis to the Northern Cod stocks, although this was not necessarily our only concern. The first day and a half of the workshop was essentially a learning exercise. We tried to organize the talks so we would get the maximum output of useful information. Because of the short time for the organization of the workshop there was some overlap between the talks. But it was better to hear things twice than not at all. The rest of the workshop was devoted to discussion of the points raised by the speakers. This generated a tremendous amount of useful information. The final afternoon was devoted to formulating specific research recommendations. For this we were able to call on a vast body of information that represented the combined experience of the many internationally respected authorities who attended the workshop. We would not go as far as to say that the workshop recommendations are the last word on the subject of the biomass spectrum and fisheries, but we are prepared to state that they represent the present "state of the art" with respect to understanding the interactions between the study of ecology and the practical administration of fisheries, particularly the fishery for the Northern Cod.

ABSTRACTS OF PAPERS

Towards a theory of the body-size spectrum of biomass in aquatic systems

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As growth-rate is allometrically related to size, in a biomass spectrum the production to biomass ratio (P/B) will decrease systematically with size. One can therefore produce a P/B spectrum that will have a negative slope, and this is essentially a reflection of a biomass spectrum, with little or no slope. However, the P/B within trophic groupings (or individual species) does not follow the same slope as the P/B for the whole ecosystem. The slopes are steeper. This means that if we plot a P/B spectrum for a complete community we will get a line with a more or less well defined slope (the line of "physiological" scaling), but if we superimpose on this the P/B spectra for trophic grouping they will lie "en echalon" across this line (lines of "ecological" scaling). If we translate these secondary lines of ecological scaling back onto the biomass spectrum we find that they produce a series of discrete domes of biomass.

The important feature of the ecological scaling is that it appears only when data are grouped according to a similarity of production efficiency (P/B), and the implication of the correspondence of the secondary P/B lines and the domes on the biomass spectrum is that it provides us with a clue as to what factors must be controlling the observed equilibrium densities. The densities that we see in the separate parts of the biomass spectrum must be related to the day-to-day activities of the individual organisms in satisfying their food requirements. These are daily energy balances, which add up to seasonal patterns by appropriate weighting of the sampling of ecosystems. This puts studies of biomass spectra on a practical time-scale, related to the short term dynamics of the ecosystem. This short term time scale is very different from the long term equilibrium scales that underlie the primary scaling.

We can conclude that within the general conditions of productivity defined by the biomass spectrum it is the secondary scaling of the biomass that reflects system production changes at the shorter time scales represented by fish. We would expect larger changes in biomass, and possible smaller changes in production, with body size (due to fishing?) than are predicted by the primary slopes. We do, however, need more experience in describing biomass spectra to see the kinds of changes that are measurable in the short-term, but the time-scales of the underlying mechanisms suggest that they should reflect year to year or seasonal changes in ecosystems. The production parameters reflected in the biomass spectrum put studies of production relations on a

unit area basis, and are thus related to the average density of the stocks. It is essential to transform these density measures into abundance information over the whole area occupied by the stock if spectrum information is to be usefully compared with predictions of production and yield based on fisheries data. Fisheries data assume that the whole population has been sampled, the biomass spectrum assumes that the representative area has been sampled.

Dynamic simulation modeling of biomass spectra

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Research on biomass spectra has progressed from the empirical discovery of the linear biomass spectrum by Sheldon and his colleagues, to bioenergetic models developed to explain the regularity of the biomass spectrum, to models that include dynamic variability of biomass distributions, finally to models exploring the full spatial and temporal variability of the biomass spectrum. There have also been studies of the biomass structure of systems in which the spectrum is not linear, notably the benthos. As these models have become more detailed they have also become more complex, and it is no longer possible to find analytic solutions to the model equations for most systems that are realistic.

An alternative to detailed analytic solution is computer simulation. This approach lacks elegance but has enormous power to incorporate detailed physical and biological descriptive information. An example is presented of a generic continental shelf model. Three size classes are considered that correspond roughly to large fish, small fish and zooplankton. The large fish are assumed to be demersal and capable of feeding on both small fish and macrobenthos, while the small fish are pelagic planktivores. During the first half of the simulation the demersal fish recover rapidly from low levels, while the pelagic fish and the zooplankton oscillate annually about steady mean values. Subsequently, the large fish biomass declines, the pelagic fish stocks crash and the zooplankton increase. The pattern looks very like what one would expect from a sudden jump in pelagic fishing effort, leading to food limitation for the large fish, but there was no change in fishing mortality in the simulation. The explanation lies with the dynamics of the benthos and with the benthic-pelagic coupling. During the first part of the simulation the demersal fish feed on macrobenthos, and the drop in fish biomass halfway through the simulation is a result of a crash in the macrobenthos followed by a feeding switch of the large fish from benthos to pelagic small fish.

We should note that the parameters in this simulation are not well known, and this particular simulation may not mirror the Northern Cod ecosystem. It is presented to show how bioenergetic simulations based on the biomass spectrum can lead to an understanding of overall system dynamics. It also shows how models of this type could alert us to the possibility that potentially major changes in fish stocks could be brought about by subtle changes in the coupling between important subsystems.

It is unlikely that bioenergetic models will ever provide a complete alternative to population-dynamics based models for stock assessment. Stocks are governed by bioenergetics, but they also depend on species or environmentally related factors such as recruitment success. However, for the Northern Cod ecosystem, size-based computer simulation models can be a valuable complementary approach to traditional stock methods and can play a major role in understanding ecosystem dynamics.

Biomass spectra as indices of ecosystem production in relation to fisheries yield

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It has been suggested that pathways of energy flow from primary producers to higher trophic levels can be studied using the biomass spectrum approach. In the work described here biomass spectra were generated for six environments to show that 1) the levels of phytoplankton and fish density are highly correlated, 2) the slope of the biomass spectrum is constant, suggesting similar energy transfer efficiencies among ecosystems with varying levels of biomass density, and 3) that the intermediate trophic pathway between phytoplankton and fish is highly variable, being comprised of varying proportions of benthos and zooplankton, depending on the physical structure of the ecosystem. It is clear from this study that the biomass spectrum approach provides a useful framework within which fisheries production and yield can be determined from measures of primary production. At the same time it provides insight into the mechanisms that underlie fisheries yield.

Microplankton biomass distributions of three contrasting ecosystems in the southern Benguela region

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A size-based model is used to simulate biomass fluctuations of four size classes of autotrophs and five size classes of heterotrophs in microplankton communities. Most of the parameters in the model were either derived using size regressions or represent best estimates of constant processes. It was applied to three contrasting ecosystems in the southern Benguela region of South Africa; an upwelling region on the west coast, a stratified region on the Agulhas Bank and an oligotrophic region of the south east Atlantic Ocean. The models were identical except for the rates of new nitrogen input and the ambient temperatures. For the nitrogen input, the upwelling model had a single large pulse, as would occur in nature, while the other two had slow steady inputs. The ambient temperature of the upwelling model was set at 10^0C, followed by the Agulhas Bank (20^0C) and the oceanic (25^0C) models.

The outputs of the models represent biomass changes over time. The upwelling model depicts the growth and decay of a phytoplankton bloom over 15 days, much as it occurs in nature after an upwelling event, and the heterotrophs in this model undergo large fluctuations, especially at the larger sizes. In the Agulhas Bank model the autotrophs undergo a number of fluctuations during a 30 day period, although the overall standing stocks remain fairly constant. In the oceanic model the plankton reaches a steady state after about 30 days, when the community is dominated by the two smallest autotroph and the three smallest heterotroph size classes. In all three models small organisms show more rapid population growth and more frequent population fluctuations. However, the magnitude of the changes is less than for larger organisms, especially large autotrophs.

To assess the "average" structure of these rapidly changing model communities, biomasses were averaged over time. The results indicate that the upwelling model is dominated by large phytoplankton and large heterotrophs whereas the Agulhas Bank model has a relatively even distribution of biomass. The oceanic model is dominated by the smallest phytoplankton.

Thus, differences in nitrogen supply rates produce very different size structures for the plankton communities, and these in turn will affect the size structures of the pelagic fish populations. In systems with short food chains (e.g. in upwellings) the phytoplankton community is dominated by large cells and the biomass distribution is not flat. This is important because phytoplankton sizes determine the lengths of the food chains to

pelagic fish. Detailed size structures of phytoplankton communities may be overlooked if a bigger log scale were used to represent the size classes. In the models discussed here a log scale to base 5 was used. This is biologically meaningful because most predator-prey ratios in the microplankton are of this order.

To assess the functioning of the three model communities all carbon and nitrogen flows were averaged over time. In all three models the smallest autotroph size class was the largest contributor to carbon fixation, despite the fact that large cells dominated the biomass in the upwelling model. In general, biomass distributions are not good indicators of the relative importance of different size classes in ecosystem processes. In all three systems it was found that, on average, most carbon entering the system was dissipated after three trophic transfers. This may indicate that short food chains with large phytoplankton cells at their base should be most efficient for transferring primary production to pelagic fish. Thus, the size distribution of phytoplankton is important for ecosystem functioning.

Size structure of the southern Baltic ecosystem

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The size structure of plankton, from bacteria to medusae, and of benthos, from meio- to macrofauna, was studied at two stations in Gdansk Basin (southern Baltic) at 2-3 week intervals in 1987. In the plankton there was a high biomass of small organisms and a low biomass of organisms larger than ca.10^8 μm^3, whereas in benthos the biomass increased with the size of the organisms. As a result, the unnormalized biomass spectra for the whole community were flat.

The values of regression parameters for the model:

$$\log(ß) = a + b(\log V),$$

where ß is normalized biomass ($gC.m^{-2}.\mu m^{-3}$), and V is body volume (μm^3), calculated from all of the data (20 sampling dates throughout the year) were as follows:

	Gulf station 92A			Open-sea station R6		
	a	b	R^2	a	b	R^2
Plankton	-0.22	-1.25	0.91	-1.20	-1.08	0.90
Benthos	-4.31	-0.65	0.82	-3.44	-0.79	0.89
Plankton and Benthos	-1.19	-0.95	0.95	-1.54	-0.97	0.94

An attempt was made to estimate fish biomass on the basis of size spectrum, according to the formula:

$$B_F = \int_{v_1}^{v_2} (V) * dV$$

where B_F is fish biomass and v_1 and v_2 are minimum and maximum fish size (volume), respectively. Estimates of fish biomass ranged from 2.7 $gC.m^{-2}1$ in the inshore Gulf station to 0.5 $gC.m^{-2}$ in the open-sea station. According to ICES WG Reports, mean fish stock (cod, herring and sprat) for the period 1978-87 in the southern Baltic (ca. 100,000 km2) was 2 million tons or equivalent to ca. 1.5 $gC.m^{-2}$, which is within the range of values estimated from the biomass size spectrum.

Particle size spectra and fish larval distributions in the Irish Sea

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As part of a program to investigate differences in fish yields and production between the North Sea and the Irish Sea we have estimated particle size spectra along a transect running from the Irish coast (Dundalk Bay) to the Welsh coast (Great Ormes Head) during the period 1987-1989. This crosses several different hydrographic regimes (coastal; stratified; mixed) with characteristic planktonic production. Fish larvae of a variety of species, including cod, are more abundant in the coastal and stratified area than they are in the deep, well mixed area; and the same is true for their prey (copepod eggs and nauplii).

A variety of methods, including particle counters (2-160 μm), nets (53 μm, 270 μm and 300 μm mesh) and a multifrequency acoustic profiling system, have been used to estimate components of the plankton system between 2 μm and about 2000 μm equivalent spherical diameter.

The main aims of the program have been 1) to develop appropriate sampling methods in relation to the important time and space scales of plankton dynamics, and 2) to investigate the relationship between larval feeding (principally by cod and sprat) and copepod abundance and dynamics.

The concentration of fish larvae in areas where their food is more abundant is primarily due to adult spawning patterns rather than larval migration or mortality. There is evidence that differences in fish production between the North Sea and the Irish Sea are a consequence of events during the first year of life. One must therefore question what the appropriate spatial and temporal averaging for biomass spectra should be, particularly if the principal processes governing fish production occur in certain physically defined areas at particular times of the year.

Length abundance and distributions of demersal fishes on the Scotian Shelf

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Biomass distributions as a function of body size (biomass spectra) have recently attracted interest as a complementary technique to typological methods of describing fish production systems. My study is aimed towards determining whether demersal fish assemblages on the Scotian Shelf display a characteristic biomass spectrum over the Shelf as an entity, and whether the observed pattern persisted at more local scales. I analyzed data taken from the 1988 summer groundfish survey of the Department of Fisheries and Oceans. Biomass distributions were estimated by plotting log aggregate numbers of all fish species combined against body length intervals. With one possible exception, the results for ten sampling areas strongly support the supposition that characteristic linear relations between biomass and body size are found for the major demersal fisheries of Atlantic Canada. The most remarkable feature of these results is that an orderly size spectrum exists, not only for the demersal fishes of the Shelf as a whole, but also at the finer geographic scale of the individual fishing banks within the region. This attests to an unexpected power of size spectrum analysis in fisheries, even at localized geographic scales. The implication of these results is that it seems that fish production processes act to spread biomass evenly across the potential spectrum of body sizes, irrespective of individual species differences in ecological adaptation.

Effects of fishery exploitation on the size structures of Northern Cod stocks: a preliminary analysis

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Application of biomass size-distribution analyses to the Northern Cod (*Gadus morhua*) fishery presupposes that fishery exploitation causes characteristic changes in the size structure of the affected stock. In order to verify this, an unexploited cod stock from Ogac Lake, Baffin Island, was compared to an exploited stock sampled by the inshore trawl fishery of region 2J.

The principal size-related characteristics of the unexploited Ogac cod are 1) a very weak association between body size and age, and 2) sexual maturity not achieved before body lengths of 65 cm in males and 85 cm in females. These features are quite different from the 2J cod, or other stocks of exploited cod. The differences in the Ogac cod are associated with an unusual trophic structure. Ogac cod less than 20 cm fed on small invertebrates, principally *Gammarus* as do small cod in exploited populations; but cod in the size-range 20-40 cm existed on an atypical diet of sea urchins. This group grew very slowly. The Ogac stock also contained a small component (about 500 individuals) of fast growing fish that achieved lengths greater than 60 cm. These fed almost exclusively on a larger component (about 10,000 individuals) of cod in the 20-40 cm length range.

I used data for the Ogac cod as input to a bioenergetic model that I had originally developed for the North Sea. The measures of growth efficiency generated by the model suggest that Ogac cod exhibit two distinct patterns. The slow-growing component of the population manifests a very steep decline in growth efficiency with increasing body size, whereas the growth efficiency of the fast-growing component decreases more slowly. A similar application of the model to data for cod in region 2J yields different results. Because these cod, like exploited stocks in other areas, manifest a relatively close association between age and size, there is no difference in the decline of growth efficiency with age between the slowest- and fastest-growing components of the stock.

These observations translate into several postulates relevant to the application of size-related hypotheses to Northern Cod analyses. The first is the premise that body size and age are closely associated; i.e. that a meaningful growth curve can be fitted to

the data. The Ogac Lake data suggest that this convention for exploited cod populations does not apply to an unfished stock. There are no data for other commercially unexploited marine stocks, but the Ogac observations are consistent with the observed size compositions of unfished lake trout and whitefish stocks. A further consideration is the advanced size at maturity of the Ogac stock. This is presumably a reflection of selection pressures that are quite unlike those experienced by an exploited stock. There is also the question of the impressive mortality, entirely due to cannibalism, imposed upon the 20-40 cm cod. Other cod stocks must experience similar vulnerability to predation during the stage of wide-ranging dependence on the benthos, but the published literature makes no particular note of it. Is the extreme vulnerability of the Ogac cod an anomaly unique to that ecosystem? Finally, although other questions could be raised, there is the apparent absence of the "smoking pistol" in the form of recruitment limitation.

Most analyses of cod, or other marine populations of fishes, deal extensively with recruitment as the factor limiting stock production to the fishery, but the Ogac situation provides no hint of such a limitation. It seems that pre-recruits are available in abundance, but opportunities to recruit to the reproducing size class are hindered by density-dependent restrictions to membership of that class. Natural mortality apparently limits the abilities of benthivore cod to recruit to the piscivore (cannibalistic) segment of the population. This difference, between exploited and unexploited cod stocks, may well comprise the single most meaningful distinction that can be applied to the fishery of the Northern Cod. The imposition of a fishery on an unexploited cod stock may bring about substantial changes in stock dynamics. These could include, 1) elimination of natural mortality on the larger individuals as a primary control on recruitment, 2) decreased abundance of the smaller individuals most vulnerable to predation (including cannibalism), and 3) increased dependence of stock abundance on the annual success of reproduction. It also follows from (3) that we would see a greater dependence on density independent (abiotic) factors for determining annual stock variation.

The size-dependent signatures of such changes, as a consequence of exploitation intensity, should result in 1) a marked decrease of size-at-age variability, 2) selection for a decreased size at maturity, and 3) increased dependence of interannual variability on the survival of pre-recruits. A critical assessment of the strengths and variabilities of these size-dependent signatures could well provide valuable information on the effects of the fishery on exploited stocks of Northern Cod.

Biomass size-distribution and metabolism in the pelagic zone

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During the past 20 years, there has been an increasing interest in the size-structure of living matter in aquatic ecosystems. The distribution of biomass as a function of organism size in an ecosystem, regardless of taxonomic criteria and without reference to the trophic level formalism, has been considered as a new way to study the structure of the pelagic ecosystem from a holistic standpoint. During the 1980's, a growing body of evidence has given further support to this approach.

In spite of growing descriptive information about the size-structure in the pelagic system, the study of the relationship between the biomass size-distribution and metabolism at the community level has largely been ignored. This information can be significant for understanding and modelling the fluxes of energy and matter in the pelagic system. The present study was designed 1) to determine the relationship between respiration and body size at the community level of organization in several pelagic ecosystems, and 2) to analyze the relationship between biomass size-spectra and metabolic size-spectra in planktonic communities.

The study was conducted during September 1990 on Georges Bank, Northeast Channel, the Gulf of Maine and the Scotian Shelf. Size classes of bacterioplankton and microplankton in the upper 100 m were determined with fluorescence microscopy and an image analysis system. Mesozooplankton samples were collected from the upper 200 m (or a few meters above bottom where shallower) and size-fractioned biomass was determined gravimetrically. The metabolic activity of different size classes was determined by ETS (Electron Transport System) methods.

The total ETS activity values for the planktonic communities studied were close to those found in other studies from the same geographical areas. The slopes of the normalized biomass spectra for the different locations ranged from -1.126 in the Northeast Channel to -0.908 in Jordan Basin. The two stations located in the Northeast Channel, which is the most oligotrophic place studied, presented the more negative slopes. The correlation coefficient (r^2) of the biomass-size spectra is highly significant

in all stations studied. The following equation describes the linear regression when the data from all the stations studied are combined:

$$Log_2(NB) = 33.99 - 0.969Log_2\ V \qquad \{N = 138,\ r^2 = 0.969\},$$

where (NB) is normalized biomass (m^{-3}) and V is body size (μm^3).

The metabolic size-spectrum for every station can also be properly described by straight lines. The metabolic-size spectra for all stations can be described by the following relation:

$$Log_2(ETSN) = 8.518 - 1.198Log_2\ V \qquad \{N = 57,\ r^2 = 0.970\},$$

where (ETSN) is the normalized ETS activity ($\mu l\ O_2\ h^{-1}\ m^{-3}\ \mu m^{-3}$) and V is organism size (μm^3). It is important to note that in all stations the metabolic size-spectra have a more negative slope than the biomass size-spectra, indicating that the smallest organisms play even a more important role from a metabolic point of view than from a biomass standpoint. The use of biomass spectra in combination with metabolic spectra as a tool for the analysis of ecosystem is discussed.

Biomass size spectra of the Lake Michigan pelagic food web

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Biomass size spectra for the complete Lake Michigan pelagic food web from picoplankton to salmonids were constructed for nine sampling transects around the lake in May and in September, 1987. Size spectra were typical for freshwaters, having distinct peaks corresponding to major size groups. Biomass concentration of algae, zooplankton and planktivores conformed to particle-size model predictions, but piscivore biomass was lower than predicted because these species are stocked. Mean annual total pelagic biomass was 72.3g.m^{-2} compared with a predicted range of 78.8-85.3g.m^{-2}. Potential production of *Mysis* and *Pontoporeia* were in agreement with model predictions. No estimates of zooplankton or planktivore production were available, but I calculated that these could be 72.1-91.6 and 2.5-4.1g.m^{-2}.yr^{-1} respectively. Our analyses suggest that piscivore production is constrained by food web structure. Bloater, which comprise 72% of planktivore biomass, make up less than 20% of salmon diets. I estimate that piscivore production could be double the current value of 0.27g.m^{-2}.yr^{-1} if the forage fish community changes to include species more available to salmon.

Size spectra in deep demersal fishes

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The sizes attained by component species tell much about the way communities and ecosystems are structured and function. It has been shown that the production to biomass ratios (P/B) in fishes scale according to the -0.26th power of the adult weight. This relationship, applied to assemblages of mesopelagic fishes, has been used successfully to produce a chart of fish production in the open North Atlantic that mirrors in many regards the well-known chart of primary production in the ocean. The same approach should be useful for demersal fishes as well, but studies where independent confirmation of results are available have not been done. Size contains other useful information as well. There are good theoretical arguments, for example, that relate size to foraging mode and strategy.

Data on deep demersal fishes from the Porcupine Sea Bight and Madeira Abyssal Plain in the Atlantic (200-5400 m depth) are used to illustrate and investigate these points. Patterns in the frequency distribution of sizes attained by species at various depths can be related to probable feeding modes, and these are supported by direct observations on diets. Biomass spectra for the same data, and on the same size class basis, show different patterns for the slope and the rise. The biomass spectrum for the slope is a rather flat one indicating, as had been inferred from the food habit studies, that there is a relatively uniform supply of food to that region throughout the year. The pattern in the biomass spectrum for the continental rise, however, is quite spiky with a strong peak at 211 grams. The conclusion is that food sources to this region are pulsed and probably in the form of infrequent, random and rapid falls of material (such as the bodies of large macrozooplankton that die after spawning) from surface layers.

Biomass spectra and fish catches in the North Atlantic

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Four regions were investigated, each with a well established fishery. These were the North Sea, the Gulf of Maine, the Gulf of St. Lawrence and the Scotian Shelf. Estimates of average phytoplankton biomass were derived from the published literature,

and these were extrapolated to the fish size-range following the assumption that the biomass spectrum was flat. In this way estimates of fish standing stocks could be made. As the growth rates of the fish in the various fishing areas are relatively well documented, it was possible to estimate the average annual fish production for each area from the standing stock estimates. It is generally believed that to maintain a sustainable fishery somewhere between 30% and 50% of the average annual fish production can be safely taken.

For the North Sea we found that from 1930 to 1950 less than 30% of the predicted production was taken, and the fishery seems to have been stable. From 1950 to 1962 the proportion increased to 50%, and this did not seem to adversely affect the ecosystem. From 1962 to 1970 the proportion of the predicted fish production taken by the fishery increased rapidly to more than 100% and the fishery collapsed. For the Gulf of Maine the situation was similar but there was less evidence for recent overfishing. From 1930 to 1960 fish catches were less than 30% of the predicted production. From 1960 to 1970 the annual catch was around 50% of the estimated production, and while the system was no doubt stressed there was no evidence of a collapse of the fishery.

For the Gulf of St. Lawrence we tried to partition the yield of the fishery between species. This was not too difficult because there are only two fisheries of economic importance (for fin-fish), herring and cod, and these can be clearly separated by size. Our estimate of the fishery yield for herring (or fish of the same size), assuming 50% of the production could be taken, was 85,000 tons. The average catch from 1958 to 1977 was about 50,000 tons. As there are fish of the same size as herring in the Gulf of St. Lawrence (e.g. mackerel) that are not taken commercially, this probably represented the maximum sustainable yield, and the herring fishery seemed stable. The estimate for the potential fishery for cod **or fish of the same size** was 475,000 tons, whereas the average groundfish catch from 1958 to 1977 was only 150,000 tons. We concluded that fish the size of cod were underexploited in the Gulf of St. Lawrence. This was confirmed when we investigated the Scotian Shelf. Here we partitioned the fishery between herring, silver hake, cod and haddock, but because of the overlap of size between the species we had to treat the silver hake, cod and haddock as a single unit. We estimated the sustainable groundfish yield at 111,000 tons and the average for the fishery from 1954 to 1962 was 115,000 tons. It seems that the fishery was stable. The average catches for 1962-77 were, however, three times more than this. The fishery was taking more than our predicted total production and it crashed. The herring fishery followed a similar pattern. We estimated an average fishery yield of 12,000 tons. The average catch until 1968 was about at this level and the fishery seemed stable. In 1969 the catch went up by an order of magnitude and the fishery crashed. The pattern here is quite similar to that of the North Sea; overexploitation (according to predictions from the biomass spectrum) followed by a rapid decline in the fisheries yield.

When we compare the estimates and fish caught in the Gulf of St. Lawrence and the Scotian Shelf (during stable periods) we find that on the Scotian Shelf all the

predicted yield is taken whereas in the Gulf of St. Lawrence there was unexploited potential. The difference is silver hake. These were taken on the Scotian Shelf by European fishermen who had a market for them. They were not taken in the Gulf of St. Lawrence by Canadian fishermen because there was no local market for this species.

It seems that at our present level of knowledge the biomass spectrum cannot be used for year-to year management of single fish stocks. We do not have the level of resolution necessary for this. But it seems that it can be used to monitor the average health of a fishery. It would serve its purpose well if it could be used to do no more than sound a warning before a fishery crashes.

The biomass spectrum in the S.E. Atlantic in relation to historic and potential pelagic fish yields

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The Benguela upwelling system and the adjacent south and south-east coasts of South Africa may be divided into several regions based upon the physical oceanographic environment. These include the northern Benguela (Namibian) region, with a productively active area of some 130,000 km^2, and the southern Benguela region of some 40,000 km^2. Each of these is associated with a pelagic fishery, mainly for the sardine (*Sardinops ocellatus*) and anchovy (*Engraulis capensis*). In both cases there have been major declines in catches of the larger and longer-lived sardine, followed by a change to smaller-meshed purse seine nets.

Using satellite and shipboard estimates of phytoplankton standing stock, and assuming a flat biomass spectrum, the standing stocks of fish that might be caught by large- and small-meshed nets in the northern and southern Benguela regions are predicted. Assuming that 50-75% of fish in the size ranges are of commercial species accessible to the fishery, the predicted standing stocks are comparable with VPA estimates for the Namibian (northern) region and slightly above the VPA estimates for the southern region. Similar estimates of fish biomass are made for two unexploited areas on the south and east coast of South Africa.

Fish production has been estimated for each of the regions, assuming a P/B ratio of 1 for fish caught with a 38 mm mesh net. These estimates have been further extrapolated to give the potential yield for each area, assuming that 25-50% of the production can be safely harvested. These estimates are compared with mean and

maximum catches in the two regions. Mean catches lie within the predicted range, but maximum catches exceeded the predicted ranges and in both cases the sardine stock collapsed. Similar calculations were made for the 13 mm purse seine net employed since 1964, assuming a P/B ratio of 1.5 for the smaller fish that can be caught by these nets. In these cases the mean and maximum catches lie below the predicted ranges; nevertheless, there have been dramatic recruitment failures in the anchovy fishery, probably due to large-scale environmental influences augmented by fishing pressure.

Coarse measurements of biomass spectra (2-2000 μm) in the upwelling region generally show slight peaks in the 20-200 μm range during autumn, when pelagic fish recruit in the region. These may be caused by diatoms. The variable size spectra are in accord with the results of the simulation models of Moloney, which show time-varying biomass spectra in coastal waters but steady flat spectra in the open ocean. We conclude that there are some problems associated with using the biomass spectrum for fisheries management. These include, 1) spatial variability of plankton and fish stocks; not all stocks in a size range are accessible to a fishery, and 2) temporal variability of fish stocks in relation to large scale physical forcing; exemplified by the sardine-anchovy "flip-flop" and by the relation of hake recruitment to sea surface temperature in the Benguela region. Thus, data on biomass spectra need to be integrated both spatially and temporally, and the method is presently limited to "ball-park" estimates of total yield based on the primary flat biomass line. It is not yet suited to year-to-year single species management. However, the biomass spectrum has a sound theoretical base (unusual in fisheries ecology) and can be modeled dynamically. It has distinct promise for the future once the dynamics of the "Dickie Domes" are better understood.

The allometric determination of pelagic production rates

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Data on the species size distribution of the pelagic community in the Celtic Sea was reviewed. The main features are a fairly even distribution in all size classes of pelagic autotrophic organisms but five size classes of pelagic heterotrophs, separated by approximately 10^3 differences in individual weight. In contrast, data for benthic organisms showed three size modes, which corresponded with the troughs in the pelagic spectrum. The constraints on body size appear to be different in the two systems and their appeared to be little evidence for coupling between the pelagos and the benthos which might result in complementary patterns of size distribution, except perhaps for interactions between the pelagic larvae of macrobenthos and the permanent macrozooplankton at the upper end of the size spectrum.

Allometry was then discussed as an accurate method of estimating the productivity of natural assemblages of phytoplankton cells of >5 μm in diameter. The ^{14}C fixation rates of phytoplankton cells, measured over a five year period in the Celtic Sea, were used to test the relationship between cell size and productivity of natural phytoplankton assemblages. Phytoplankton biomass was estimated using computerized image analysis to estimate cell volume. These biomass estimates explained 85% of the variance in ^{14}C fixation rates under optimum growth conditions; in comparison, chlorophyll concentration explained only 59% of the variance. An allometric model, based on literature values for the relationship between cell size and specific growth rate, was applied to the estimated cell volumes for each individual phytoplankton in natural assemblage and was used to estimate the potential productivity, under optimal growth conditions. This allometric estimate of phytoplankton productivity explained 93% of the variance in *in situ* ^{14}C fixation rate. The method was then extended to estimate picophytoplankton productivity; the allometric model again explained 90% of the variance in the *in situ* ^{14}C fixation rate, under optimum growth conditions.

When applied to data obtained on 4 consecutive days at the same station in the Celtic Sea, estimates could be made of the growth rate of individual phytoplankton species. Estimates were also possible of the presumed losses from day to day due to the processes of sedimentation and grazing. However, although the approach appears to work well with autotrophic phytoplankton, when applied to heterotrophic microbes, the allometric model estimates high potential growth rates of bacteria and protozoa which may be difficult to sustain in natural assemblages. The best allometric description of natural systems is obtained when a value of -0.15 is taken for the exponent of the allometric equation, rather than the generally accepted value of -0.25 for the mass-dependent rate, suggesting that the size dependence of marine microbes may be less strong than for other aquatic organisms.

The physical environment of the Northern Cod ecosystem

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Understanding the dominant characteristics of the physical environment of the Labrador and Newfoundland Shelves is necessary for the planning and implementation of a biomass spectrum analysis of the northern cod ecosystem. The oceanographic environment of the region is influenced by the bathymetric features of the shelf, meteorological factors, ice dynamics, and the exchange of mass, heat and salt between the shelf and the adjacent water bodies. Recent analysis of the data collected from the Labrador and Newfoundland Shelves reveals a complex ocean environment that is highly variable; an overview of the physical environment and present state of knowledge of its

variability is discussed. Data gaps are identified, and the physical oceanography programs established as part of the northern cod science program to develop a better understanding of the oceanographic influences on the cod ecosystem dynamics are described.

Patterns of recruitment variation: influence of life-history and environments

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The groundfish communities on the Labrador shelf were compared with similar ecosystems in other regions in the North Atlantic.

Species diversity for depths greater than 200 m: there is similar species diversity from Cape Hatteras to Northern Labrador, i.e. about 10 species per research vessel tow. Species diversity for depths less than 200 m: species diversity, in terms of species per research tow, is about one third less than that found on Georges Bank and the Scotian Shelf.

Cod forms an important part of the catch from research vessels in all size classes, and dominate larger size classes in region 3L. Redfish and American plaice become more important for smaller size classes.

Cod is more important component of the groundfish community in NAFO region 2J3KL than in more warmer regions, where other gadoids, e.g. pollock or haddock, form an important part of the community.

Density and environmental temperature appear to have an important effect on growth of cod in the 2J3KL region. There is no evidence that the abundance of the major prey item of cod, i.e. capelin, have any effect on cod growth. Landing in 2J3KL are dominated by groundfish species, particularly cod, while landing in warmer regions have a larger pelagic component.

Pelagic fish populations of the Grand Banks region

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Capelin, herring and mackerel constitute the three main species exploited by pelagic fisheries in the Newfoundland area. Both herring and mackerel have a long history of commercial exploitation with catches ranging upwards to 30,000 tons. These fisheries are entirely coastal and reflect the nearshore distribution of these species. Capelin, on the other hand, have only been exploited on a commercial basis since the early 1970's when offshore fisheries produced catches of 300,000-400,000 tons annually. These offshore fisheries have all but disappeared with the extension of jurisdiction by Canada in 1977. New fisheries mainly for roe capelin in inshore waters, developed in the early 1980's and now exceed 100,000 tons in annual removals. With the biomass levels in the range of 5-10 million tons, exploitation levels remain low and all abundance indices indicate that capelin biomass levels have risen steadily during the last pentad, reflecting improved recruitment.

The production system supporting cod in Division 2J3KL

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Most of the food consumed by cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland (NAFO Div. 2J3KL) comes from the pelagic food web. The major prey is capelin (*Mallotus villosus*). Additional important prey include other planktivorous fish (primarily arctic cod (*Boreogadus saida*) in the north and sand lance (*Ammodytes* sp.) on Grand Bank), large zooplankters (notably euphausiids and hyperiid amphipods) and benthic crustacea (mainly shrimp and crabs). The only prey species that is monitored over broad spatial scales is capelin. Arctic cod and sand lance are taken only as small by-catches in research vessel surveys. Pink shrimp (*Pandalus borealis*) and snow crab (*Chionoecetes opilio*) are monitored only in commercial fishing areas. Little is known of the species composition, distributions, life cycles and production of macrozooplankton. In the absence of independent estimates of distribution and abundance of the prey of cod, it is difficult to study feeding selectivity of cod and to seek empirical evidence of predator-prey and competitive relationships.

A monitoring program is in place to determine the relationship between capelin abundance and the feeding by cod on capelin and alternate prey. An analysis of the data

collected in Div. 2J3K during the autumn of 1978 and 1980-86 revealed that the quantity of capelin in cod stomachs increased with capelin abundance. There was no evidence that cod compensated during a period of low capelin abundance by feeding more intensively on other prey. The quantities of benthic prey (mainly pink shrimp and snow crab) in the cod stomachs remained relatively small in all years. The quantities of alternate pelagic prey (mainly hyperiids and Arctic cod) were more variable, but much less variable than the quantity of capelin. Even though hyperiids are prey of capelin, and Arctic cod is a potential competitor, both appeared to vary independently of capelin.

The most intensive feeding by cod does not necessarily occur in the same geographic areas as the most intensive primary production. Production may be moved spatially as it moves to higher levels of the food web. The most dramatic example in the Newfoundland-Labrador area is the migration of maturing capelin from offshore feeding areas to coastal waters to spawn in late spring and summer. Large numbers of cod migrate from offshore waters to take advantage of the dense aggregations of capelin in shallow water. The study of cod migration and production may be greatly aided by study of how its dominant prey species attune their feeding and reproduction to the physical and biotic cycles of the Newfoundland Shelf.

Investigating the effects of the Hudson Strait outflow on the Labrador Shelf using the biomass spectrum

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It has been suggested that vertical mixing in Hudson Strait produces nutrient rich water that is advected onto the Labrador Shelf. This nutrient flux could give rise to increased primary production which would support a developing food chain as the water moves south along the shelf. If this hypothesis is correct then an increase in the larger-sized pelagic organisms would be expected downstream from Hudson Strait. To test this hypothesis physical, chemical and biological data (including particle size spectra) were collected along the Labrador Shelf, from Saglek Bank to Hamilton Bank, in September 1985.

Reduced stratification, indicating recent mixing, was observed on Saglek Bank, and stratification increased progressively towards the south. The highest nutrient and

chlorophyll levels were found on Saglek Bank, with localized patches also occurring on Nain Bank and along the continental slope. High nutrient and chlorophyll levels were also observed in the marginal trough inshore of Hamilton Bank.

Particle size spectra for the size range 1-1028 μm were measured at 26 stations. On the banks the spectra were relatively flat between 32 and 1028 μm with average standing stocks of 0.1g.m^{-3} (wet weight) on Hamilton Bank and 0.2g.m^{-3} on Saglek Bank. Standing stocks were lowest over the continental slope and in the Labrador Sea. The highest standing stocks occurred in the 509-1028 μm size range at the stations nearest the coast between Nain and Makkovik. There was no systematic change in the average slope of the size spectrum from north to south, as would have been expected from a developing food chain. The most striking change was in the planktonic herbivore concentrations which were high inshore and low offshore.

Four major faunistic patterns could be detected in the plankton. 1) In the Labrador Sea *Metridia longa*, *Conchoecia* sp., tintinids and *Ceratium* sp. were dominant. 2) The Labrador Current was characterized by *Globigerina* sp., *Limacina helicina* and *Rhizosolenia* sp., and these were also found occasionally between the banks in the marginal troughs. 3) Some species, such as *Calanus finmarchicus* and *Oithona similis* were abundant in the Labrador Sea but extended onto the continental shelf. 4) Other species of more arctic character, such as *Pseudocalanus* sp. and *Calanus glacialis* were most abundant inshore but extended onto the banks. No gradation was seen in the abundance of the various copepod development stages from north to south. Our results demonstrate that physical mixing in Hudson Strait gives rise to high nutrient levels on Saglek Bank, and this in turn enhances plankton production. However there is no evidence to show that this high production supports a food chain that is advected southeastwards along the Labrador Shelf.

Quantitative survey data for benthic production estimates

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The estimation of total benthic community production over large areas is difficult. Quantitative estimates of standing stock are laborious and time consuming because of the high species diversity and spatio-temporal heterogeneity of the benthos; but it is possible to make reasonable estimates of standing stock from surveys that cover large areas, and this can include seasonal coverage. A number of measurable attributes

of benthic animals have been shown to be allometrically related to their annual, size specific, production (P/B). It is possible, therefore, to estimate benthic production from survey data.

Conventionally, estimates of species P/B are based on measurement of maximum life-span, but this requires both species identification and estimates of maximum life-span, and there are several shortcomings in this approach. Life-span is not a conservative life-history trait. A small error in estimation, especially for short-lived organisms, can produce a large error in the estimate of production.

As an alternative, we have developed a method for measuring benthic community production based on biomass and size-structure. This has so far been used only to measure macrofaunal community production. Community production was calculated from the size structure of the whole community by applying the allometric regression of P/B on body size to the biomass size-distribution. The total biomass of each size class was multiplied by the P/B for that class and the resulting production values for all size classes were summed to give an estimate of macrofaunal community production. Similar calculations can be made for each species and the community production can be estimated by summing the contributions of each of the species in the community instead of the size-groups. Both methods produced similar results but the values obtained were about half those obtained from the conventional methods.

The problem seems to lie with the estimates of maximum life span required by the conventional methodology. These are mostly literature based and most of the data were collected in northern Europe and the United States, where water temperatures are generally higher than in the Newfoundland region.

It would seem that it will be only by applying the size-structure approach to estimates of benthic production will we obtain reasonable estimates of benthic production, and thus reasonable estimates of the input of the benthos into the Northern Cod system.

Size- and biomass-distribution of pelagic zooplankton on the SE Shoal of the Grand Bank

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Plankton surveys employing a 50 station grid (18.5 km spacing) located between 43.5^0 N and 45.0^0 N, and between 49.0^0 W and 51.0^0 W on the SE Shoal of the Grand Bank were conducted in September of 1987 and 1988. Zooplankton were sized using a calibrated optical particle counter (600-30,000 μm equivalent spherical diameter) mounted on a miniBIONESS 7-net sampler which was towed at ~1.5 m/s in a stepped oblique manner from near-bottom (max 70 m) to near-surface (2.5 m). Temperature and salinity data were collected with a CTD mounted on the miniBIONESS which was employed to collect capelin (*Mallotus villosus*) larvae. Temperature and salinity data showed similar patterns in both years and defined a N-S oriented sub-thermocline front near the eastern side of the grid at the shelf break. This front separated cold (0-2^0 C) Labrador Current water (seaward of the shelfbreak) from a warmer (4-5^0 C) water mass in the 30-60 m depth stratum centred over the shoal. There was evidence of a cold (<3^0 C) water mass intrusion on the western side of the survey grid in both years.

The distribution of size-structured biomass was highly variable in the horizontal (~20 km resolution) and vertical (~5 m resolution) planes, as well as between years. The 1987 depth and station averaged biomass size-distribution showed a maximum of 0.05 g m^{-3} in in the smaller (800-1000 μm ESD) size-class, 0.005 g m^{-3} in the medium (2000-4000 μm ESD) size-class, and 0.025 g m^{-3} in the larger (5000-7000 μm ESD) size-class. The 1988 depth and station averaged biomass-distribution was similar with a maximum of 0.04 g m^{-3} in the smaller size-class and 0.005 g m^{-3} in the medium size-class, but showed a greatly reduced concentration of 0.01 g m^{-3} in the larger size-class. The "normalized" biomass-distribution (600-30,000 μm ESD) had a slope of -0.80 in 1987 and -0.67 in 1988. The standard ("un-normalized") distribution had a slope of -0.164 in 1987 and -0.038 in 1988, and neither were significantly different from zero. However, the distributions in both years showed "wave-like" deviations from the slope predicted from biomass size-distribution theory.

The distribution of particle biomass in the 600-1000 μm ESD size-class (potential prey for 20 mm capelin larvae) was also highly variable in the horizontal and vertival planes. Biomass concentations in the 1000 μm ESD size-class reached 0.06 g m^{-3} in the 30-35 m depth stratum on the western size of the grid, 0.14 g m^{-3} at 30-35 m in the centre of the grid, and 0.37 g m^{-3} at 25-35 m at the sub-thermocline front near the shelf break on the eastern side of the grid. Depth-averaged biomass concentration of the 100 μm ESD size-class ranged from 0.01 to 0.03 g m^{-3} on the western side of the grid, from 0.01 to 0.06 g m^{-3} over the centre of the shoal, and from 0.04 to 0.12 g m^{-3} on the east side of the grid (at the front). Biomass concentrations in the 600-1000 μm ESD size-classes showed a general sub-thermocline west to east gradient from 0.08 g m^{-3} to 0.6 g m^{-3} at the front in 1987, and similarly from 0.08 g m^{-3} to 0.360 g m^{-3} in 1988. The concentration of capelin larvae (20 mm average size) was not correlated with the biomass of the 600-1000 μm ESD particle size-class. However, the spatial disribution of larvae in better-than-average condition (as determined by lipid content) was coincident with regions of high biomass in the 600-1000 μm ESD size-class, which was coincident with the frontal region.

It is concluded that further development of the biomass "spectrum" theory will require quantitative observations directly from the field, and must begin to seriously account for the spatial (vertical and horizontal) and temporal (at least seasonal) variability that is clearly related to variations in water mass characteristics (temperature and salinity). It is further hypothesized that interannual and spatial variations in selected ranges of the biomass size-distribution (e.g. potential prey sizes) are necessary and sufficient to explain variations in the condition and thus survival probability of fish larvae. This approach, and rigorous testing of the hypothesis, may lead to substantial improvements in recruitment and stock-size forecasting.

SUMMARY OF THE STRUCTURED DISCUSSIONS

How well can we extrapolate from the size distribution of small organisms to estimate fish stocks?

W. G. Sprules (Rapporteur)

1) Estimates of small particle abundance must be averaged over the spatial and temporal scales at which the dynamics of the target size groups (fish) are operating.

2) There is a need for greater understanding of mechanisms controlling the shape and dynamics of particle-size spectra, particularly the "Dickie Domes" (see "**Abstracts**"), to strengthen the confidence we have in predictions about fish stocks.

3) One useful approach could be to compare particle-size model predictions of total density of fish in a particular size range with the sum of the VPA estimates for the component species of that size interval. If the two estimates agree, confidence is gained; if not, potential errors in the estimates are indicated. Particle size models should be viewed as complements to, not substitutes for, VPA approaches.

4) Potentially the most useful contribution of particle-size approaches is to establish general limits to the productive capacity of a system over moderate scales of time and space. More specific predictions within these scales are best achieved with VPA models.

5) Particle-size models make predictions about **size ranges** of fish, not particular species of fish. Their utility in multi-species fisheries may thus be low. However, it appears that most fish on the Labrador Shelf above a particular size are cod, so particle-size models may in fact be quite useful.

6) Particle-size model estimates of fish biomass must include standard errors to be of any use.

7) Some evidence suggests that phytoplankton may be a better starting point than zooplankton for particle-size model predictions of fish biomass. Because of their intermediate position in the food webs, zooplankton abundances may show little discernible patterns because they reflect opposing forces operating from above and below the food web.

8) The shape and positioning of "Dickie Domes" may reflect evolutionary responses

of organisms to forces operating at ecological scales.

9) There is a need to merge particle-size theory development with routine collection of survey data on phytoplankton, zooplankton, and fish. We must move ahead with development of theory and survey techniques, not just continue with older ideas.

How well can we estimate fish stocks from fisheries data?

K. Brander (Rapporteur)

Carscadden - There is still a large gap between theoreticians who are working on biomass size spectrum related work using small size particles and fisheries scientists involved with assessments. There is a large base of size-structured fish data available and the theoreticians should work more closely with assessment scientists to use the database and test linear biomass theories more extensively.

Atkinson - Sequential Population Analysis (SPA) has been used by CAFSAC to assess the status of the northern cod stock for many years. The basic models and assumption and limitations of SPA were discussed as were the commercial and research data requirements for input. It was pointed out that while biomass spectrum analysis may yield information over the longer time scale, assessments are required annually, and these include stock size in the upcoming year so that management decisions can be made. The link between the two processes may come from comparisons of the long term vs. short term predictions to check for deviations in tracking of biomass. Deviations between the two may serve as a signal for more in depth examinations.

Brander - How does one judge "how well" we need to estimate fish stocks and what do we mean by "fisheries data"? Management is principally concerned with how many fish and of what size can be caught without damage to the stock in the longer term. Many of the difficulties in estimating stocks arise for institutional reasons (the speed with which information can be translated into advice and acted on) and management problems often have little to do with biological science. Adequate short term predictions of the fish stocks can be made using existing methods and "fisheries data". Longer term prediction is very much more difficult and for this we probably need better understanding about the structure of the ecosystem, which is where biomass spectra might help. Two questions we must address: 1) are biomass spectra likely to provide better estimate of fish stocks than other population dynamics approaches? and, 2) how such a judgment can be made in practice?

Shelton - The quantification of "how well can we estimate fish stocks from fisheries data" relates to the bias and variance associated with estimates of stock size. The state-of-the-art with respect to conventional methods of estimating stock size delivers, at best, a coefficient of variation of 20%, and more commonly 30-40%. Recent retrospective analyses of ADAPT estimates also indicate significant bias. Considerable value can therefore be placed on fishery-independent methods which reduce the uncertainty with respect to stock size and yield. In a cube with axes of time, number of species, and utility, it seems likely that the biomass spectrum approach will have maximum utility in the "deep domain" (many species, long-term).

RESEARCH RECOMMENDATIONS OF THE SPECIALIST GROUPS

We have done a small amount of editing of these reports, mainly to get them into a more or less uniform style and format. But we would like to emphasize that, in spite of the many similarities in their recommendations, the three specialist groups reached their conclusions independently.

GROUP I - R. J. Conover (Chairman)

Basic Considerations:

Newfoundland and its surrounding banks sits astride a major north-south current system. This system imports nutrients and the products of upstream production into Newfoundland waters, thereby considerably enriching them. But this import is very variable and extremely sensitive to climatic events. Therefore, any research program should include upstream monitoring to facilitate prediction of the effects of this north-south flow on the Northern Cod ecosystem. Following this general train of thought, the significance of large space-time variance was discussed, and a case was made for developing a research programme to refine biomass spectrum theory in order to incorporate spatial and temporal variability on a scale useful for dealing with the Northern Cod problem.

We put forward three hypotheses for testing. We were aware that proving a set of null hypotheses confounded by a complex and variable environment would not be easy, but we felt that they would give direction to the research program. Hence, we pose these fundamental questions:

1) That the biomass spectrum can be used to predict changes in the production system supporting Northern Cod.

2) That the form of the biomass spectrum is influenced by the physical oceanographic regime over definable ranges of temporal and spatial scales.

3) That bioenergetic modeling of the biomass spectrum can identify environmental factors affecting the size distribution of fish stocks that can be related to cod abundance.

Research Recommendations:

It would be most desirable to make use of the existing infrastructure, rather than develop a new one, and to closely couple biomass spectrum observations with other biological and physical data. There will have to be some process related research

dedicated to answering specific questions about the Northern Cod ecosystem but the cost of this program should be optimized. With these points in mind we suggest a three pronged attack:

1) To describe the space-time variability of the biomass spectrum, particularly at the smaller sizes.

   Automated biological sampling stations should be established at several of the current meter stations, with the object of obtaining the widest possible spatial coverage. It would be essential to have a multi-sample sediment trap at each station to monitor the input of organic production to the benthos. The stations should also be equipped with fluorescence monitors to record seasonal variation in primary production as indicated by chlorophyll. If possible, several sizes of chlorophyll bearing organisms should be monitored simultaneously. Finally, an acoustic particle counting and sizing system should be included to monitor zooplankton and larval fish. These systems should be organized so that they can be serviced at the same time as the current meters. A second phase of the automated part of the program would involve putting optical and acoustic counting equipment on survey cruises, including trawl, larval and egg surveys. This equipment should collect data when the ship is under way and should not interfere with other operations. Some time should be allotted, however, for selected collections, with the appropriate gear, to back up the interpretation of the automatically collected data.

2) To investigate the structure and functioning of a representative near shore environment for which considerable background data already exists. The reason for suggesting this program is that, on the basis of the available information, while Northern Cod spawn on the edge of the continental shelf the larvae and young fish move onshore to take up residence along the northeast perimeter of Newfoundland. Presumably, much of the feeding and growth of the cod stock takes place during this phase of the life cycle. Conception Bay could be a representative environment for this study. Emphasis would be placed on temporal variance of the biomass spectrum, with considerations of spatial variance kept to a minimum. Here it should also be possible to incorporate the demseral portion of the biomass spectrum into the framework for study, and it should also be possible to "calibrate" the biomass spectrum in terms of carbon, energy or species.

3) To develop a theoretical basis for spatial and temporal variation of the biomass spectrum. This would seek to incorporate remote sensing and climate related information into a useful framework of the biomass spectrum hypothesis. If successful, this theoretical structure, together with the results of work in 1) and 2), could be used to forecast the effect of climatic change on fish stocks.

GROUP II - L.M.Dickie, K. Brander (Co-Chairmen)

Basic Considerations:

The body-size spectrum of the biomass has been established as an effective tool for describing productive ecosystems. These include many lakes, Georges Bank, the North Sea and the Scotian Shelf, among others. It has also been used to predict fish production from a knowledge of the biomass distribution of the lower trophic levels for both continental shelf and upwelling systems. However, the effectiveness of these spectral descriptions may have depended on the fact that each system studied was, to a greater or lesser extent, a fully sampled "closed" system. Because biomass spectrum theory is not yet fully developed with respect to the temporal variation that may be involved in open systems, it is not yet possible to employ the full potential of the technique to advective systems such as the Labrador Shelf. Before using biomass spectrum theory to predict the ecosystem structure on the Labrador Shelf it may be necessary to assemble data to test the applicability of the hypothesis in that particular situation.

It was agreed that the potential of the newer aspects of the biomass spectrum methodology for providing an independent measure of the general level of production of the Northern Cod ecosystem is strong enough to justify a considerable effort to test it. However, without such a test, biomass spectrum theory could not be counted upon to offer any direct estimate of the potential production of an identified species, such as cod. The testing would require the collection of new biomass spectrum data for the Newfoundland area together with a detailed study of the fish populations based on the extensive historical data from fish survey cruises. A model for the kind of analysis required for the fish levels of the spectrum is now available from studies of the North Sea, the Scotian Shelf and Georges Bank.

Research Recommendations:

1) The historical data set available from the St.John's groundfish survey, and any other comparable data, should be analyzed following the methods of de Aracama (see "**Abstracts**"). Particular attention should be paid to determining regional and temporal patterns in size-class and biomass distributions relative to species.

2) A restricted area should be selected from the seasonal range occupied by cod, and data should be assembled to permit the construction of a full biomass spectrum. The best site for this would probably be the Grand Banks.

3) Within the selected area, for the first year of study all size elements of the system should be sampled monthly, with the possible exception of the benthos.

An attempt should then be made to compile an average annual biomass spectrum.

4) In order to minimize the effort required for (3) coordination with other studies should be considered. For instance, the initial data collection could be limited to transects occupied by other programs.

5) These recommendations are not likely to be realized with existing staff. Post-doctoral contracts were considered to be a viable option.

GROUP III - P. Shelton (Chairman)

Basic Considerations:

It is generally agreed that marine ecosystem structure can be adequately described by means of a biomass spectrum. It is also agreed that biomass projections from the levels occupied by small organisms can be used to estimate the average biomass of fish. However, it is by no means apparent that estimates of actual fish stocks derived from biomass spectrum extrapolations provide any more information than can be obtained from conventional stock analyses. They probably provide less. But it is not the purpose of biomass spectrum theory to replace conventional fish stock analysis. The advantage of biomass theory is that it can be used to give an independent estimate of average potential fish stock that is completely unrelated to any activity of a fishery. Simply put; biomass theory will tell us what, on average, a fish stock ought to be (i.e. the potential virgin stock), whereas conventional stock assessment will tell us what it actually is. This alone is sufficient justification for studying the biomass spectrum with a view to using it as a management tool. But once established, a knowledge of ecosystem structure based on the biomass spectrum will also provide a lot of information on food availability to fish at different stages in their life history. This is an added bonus.

Research Recommendations:

1) To begin with, a thorough investigation should be made of the existing data on biomass and size. Although it may not always be in a readily useable form there is a considerable amount of data available from various sources. For example, within DFO there is a huge amount of data available on fish, and the data on ichthyoplankton and zooplankton is not negligible. There are the data from the 1985 Hudson cruise, AFAP benthic data for the Grand Banks, data from the Mobil environmental impact survey, local plankton data (especially zooplankton) from the Ocean Sciences Centre of Memorial University, remote sensing data and C.P.R. data.

2) The existing theoretical models should also be reviewed and any potential applications to the Northern Cod problem should be critically examined.

3) Additional data should be collected, subject to the outcome of (1) that will enable seasonal averages to be made for biomass and size, mostly for organisms in the small size range (i.e. zooplankton and smaller). There is no need to mount a separate program to accomplish the bulk of this work. It can be done quite effectively by "piggy-backing" on other dedicated cruises. This approach also has the advantage that the biomass spectrum data are not being collected in isolation. Each year from Newfoundland alone there is the potential for over

1000 ship stops or near stops. At most of these a water sample and a short vertical haul could be made that would provide sufficient data for building a biomass spectrum over the size range from bacteria to small zooplankton. This represents three orders of magnitude and covers more than half the range from bacteria to fish.

4) Only when (1) - (3) had been shown to be viable should dedicated cruises be considered, although there may be a need for dedicated cruises to collect critical benthic information. These cruises would be needed to fill in spatial or temporal gaps. They would also be needed for special experiments of critical importance, such as the investigation of the Ogac Lake ecosystem suggested by Kerr (see "**Abstracts**").

5) The need for biological monitoring at a small number of fixed sites should be critically reviewed. This work should be fully integrated with other physical and chemical monitoring activities.

SUMMARY OF RESEARCH RECOMMENDATIONS

Considering the great diversity of interests of the workshop participants, the recommendations and ideas that emerged from the "question and answer" session and from the deliberations of the the three working groups were remarkably consistent. We summarize these as follows:

1) The clearest signal to emerge from the deliberations was the need to look at, and if necessary reprocess, existing data. There is a considerable amount of information available on particulate materials, plankton and fish in Newfoundland waters. The information is widely dispersed among government and private agencies and much of it is not in a form that is readily usable for investigations into biomass spectrum structure; but it could be fairly easily collected together and most of it could be reprocessed. This work would be fairly time consuming but very cost effective.

2) There is a need to refine biomass spectrum theory. There is no question that the basic theory is sound, but we need to know more about the role of spatial and temporal variability. The effect of environmental change should also be put on a sound theoretical basis. This work could proceed at the same time as the other projects. The requirements are for a modest level of funding.

3) To collect new data, particularly in the phytoplankton size range, with a view to refining information on spatial and temporal variability of biomass spectra. The aim would be to use these data, together with the data from (1), to establish normal range of biomass spectra for clearly defined areas of interest. It is from these that we could make predictions of average fish standing stocks. This data collection should be done in close association with other projects and the bulk of the sampling should be accomplished by "piggy-backing" on established cruises. This not only ensures maximum cost effectiveness but also ensures that the data collected are relevant. For instance, data on small particle distributions collected during a groundfish survey are more likely to tell us something about cod than data collected in isolation.

4) To carry out carefully planned dedicated cruises to solve specific problems that will have emerged from the work of (1), (2) and (3). This would essentially be a "mopping up" operation.

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